Genotypic Variability and Genotype × Environment Interactions among Switchgrass Accessions from the Midwestern USA

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PLANT GENETIC RESOURCES

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ABSTRACT

Genetic variation for economically important traits in switchgrass (*Panicum virgatum* L.) is needed to develop improved populations. Objectives of this research were to determine the genotypic variability, and the magnitude of genotype × environment (G × E) interaction for agronomic, forage quality, and biofuel feedstock traits among switchgrass accessions collected from remnant midwestern prairies. A total of 23 accessions and five check strains were evaluated in space planted nurseries at Mead, NE; Ames, IA; and West Lafayette, IN, during 1991 and 1992. Forage quality traits were measured at a vegetative growth stage and at heading. Disease ratings were taken just prior to forage harvest at heading. Forage composition was determined by near infrared reflectance spectroscopy. Across locations and years, significant variation among accessions was observed for forage yield at heading, vegetative in vitro dry matter digestibility (IVDMD), and heading date. Some accessions, such as IA34, were comparable in forage yield at heading to check strains and should be useful genetic sources of variation for this trait. Except for disease rating, G × E interactions were important for all traits. Selection among accessions for forage yield at heading followed by selection for IVDMD within such accessions should be an effective approach in utilizing genetic variation in switchgrasses from remnant prairie sites.

THE TALLGRASS PRAIRIE is estimated to have occupied over 500 000 km^2 of central North America (Risser et al., 1981), primarily in what are now the north central states of the USA. Much of this land has been cultivated so that today only remnants of original prairie remain. Switchgrass is native to the tallgrass prairie and is used for forage production and conservation purposes. Switchgrass has been identified as a promising species for fuel ethanol production from cellulosic biomass (Cherney et al., 1990; Parrish et al., 1990), a production process which is currently being developed (Lynd et al., 1991).

Genetic variation is needed to improve economically important traits of switchgrass through conventional breeding. Significant variation has been reported in switchgrass accessions for chromosome number, morphological traits such as leaf width (Nielsen, 1944), and winter hardiness (Nielsen, 1947). Newell and Eberhart (1961) found genetic variation for forage yield, as evidenced by narrow sense heritability estimates up to 0.74 in switchgrasses originating from Nebraska and northern Kansas. Talbert et al. (1983) reported narrow sense heritability estimates of up to 0.83 for IVDMD and 0.59 for forage yield in switchgrass germplasm from the southeastern USA. Cornelius and Johnston (1941) and Newell and Eberhart (1961) reported differences in rust reaction (incited presumably by *Puccinia graminis* Pers.:Pers.) for switchgrasses from the Great Plains region. Taller, coarser stemmed types were generally more rust resistant than shorter, finer stemmed types. Barnett and Carver (1967) later classified these as lowland and upland types, respectively.

Except for the cultivar Cave-in-Rock, which originates from a southern Illinois population, switchgrass germplasm from the midwestern states is not readily available at the present time. Most switchgrass cultivars are based on germplasm originating from the Great Plains, with examples being Pathfinder (Newell, 1961), Trailblazer (Vogel et al., 1991), and Kanlow (Hanson, 1972). Also, the origin of some switchgrass cultivars, such as Blackwell (Hanson, 1972) and Alamo (Allen, 1978), can be traced to a single female parent. Early switchgrass germplasm collections, like that of Nielsen (1944), have been lost. With the exception of Cave-in-Rock, none of the 178 accessions listed in the National Plant Germplasm System originate from the midwestern states of Missouri, Iowa, Illinois, or Minnesota. In this region, hundreds of privately and publicly owned remnant prairie sites can be found. Such remnant prairies may be useful sources of germplasm for switchgrass breeding programs.

Differential response of genotypes to various environments is an important consideration in plant breeding. Significant population × year (P × Y) interactions have been reported for seed and forage yield of Great Plains switchgrass germplasm (Eberhart and Newell, 1959), and for xylose concentration in germplasm from the southeastern USA (Godshalk et al., 1988). Evaluation of switchgrass accessions at multiple locations has not been reported previously.

Objectives of this research were to (i) determine genetic variability for agronomic and forage quality traits among switchgrass accessions collected from remnant midwestern prairie sites; and (ii) to determine the amount of genotype × environment interaction for such traits across midwestern environments for these accessions.

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Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; IVDMD, in vitro dry matter digestibility; G × E, genotype × environment; NDF, neutral detergent fiber; NIRS, near infrared reflectance spectrophotometer.

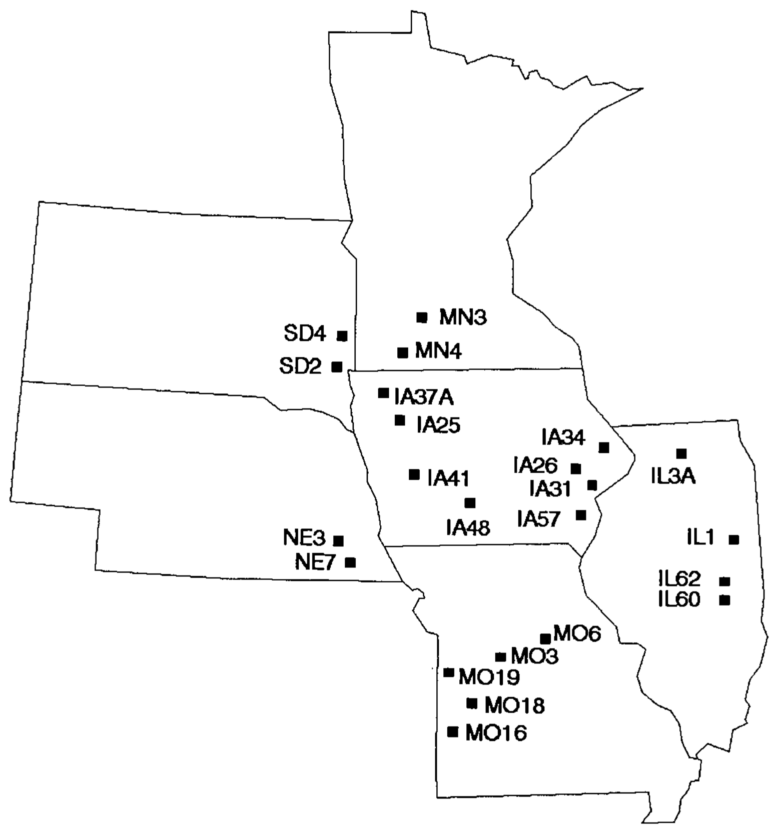

Fig. 1. Switchgrass accession collection sites. Accessions are designated by the collection site code (e.g. accession MO3 collected from site MO3).

MATERIALS AND METHODS

In this report, *site* refers to the area from which seed was collected, *location* refers to the three areas (Mead, Ames, and West Lafayette) where the experiments were planted, and *populations* refers to all 28 strains included in the research. Accessions are designated according to the site from which they were collected, e.g., accession MO3 was collected from the site MO3.

Switchgrass seed was collected in 1989 from remnant prairie sites (Fig. 1) in the North Central USA (Vogel et al., 1992). The accession IL62 was collected from a restored prairie planted during the 1940s; all other accessions originated from unplanted, native prairie sites. The accessions are a random sampling of germplasm from the numerous remnant prairies in the midwestern USA.

Seed was wet chilled for 3 wk at 4.5°C and planted in February in the greenhouse into plastic seedling tubes (22 cm deep, 4 cm in diameter) which contained a mixture of 2:1:1 soil/peat/vermiculite. Seedlings of five check populations (Table 1) and 23 accessions were transplanted near Mead, NE, on 23 May 1990, near Ames, IA, on 7 June 1990, and near West Lafayette, IN, on 12 June 1990. Soil type was Sharpsburg silt loam (silty clay Typic Argiudoll) at Mead, Webster silty clay loam (fine-loamy, mixed, mesic Typic Haplaquoll) at Ames, and Xenia silt loam (Typic Haplaquoll) at West Lafayette. The experimental design was a randomized complete block (RCBD) with two replicates (blocks) at each location. A plot consisted of a single row of 10 plants spaced on 1.1-m centers and represented a collection site or check strain.

At Mead in 1990, 2.2 kg active ingredient (a.i.) ha^{-1} of atrazine, [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5,-triazine-2,4,-diamine], was applied on 30 May, 2.2 kg a.i. ha^{-1} of metolachlor, [2-chloro-*N*-(2-ethyl-6-methyl-phenyl)-*N*-(2-methoxy-1-methylethyl)acetamide], was applied on 12 June, and 16.7 g a.i. ha^{-1} of chlorsulfuron, [2-chloro-*N*-[(4-methoxy-6-methyl-1,3,5,-triazin-2-yl)-aminocarbonyl]benzenesulfonamide]], was applied on 7 August. Atrazine was applied at Ames on 30 May, and metolachlor plus 1.7 kg a.i. ha^{-1} atrazine was applied at West Lafayette on 15 June, 1990.

Plots were fertilized prior to spring growth in 1991 and 1992 with 110 kg N ha^{-1} applied as ammonium nitrate. In spring of 1991, the previous year's vegetation was removed by mowing. Metolachlor and chlorsulfuron were applied on 16 April, 1991 at Mead and West Lafayette at previously described rates. At Ames, 2.8 kg a.i. ha^{-1} metolachlor was

Table 1. Origin of five switchgrass populations used as check strains in the multiple location evaluation of switchgrass germplasm collected from remnant prairies.

Population	Origin
Cave-in-Rock	Lowland type from southern Illinois, developed by SCS PMC†, Ellsberry, MO.
Cave-in-Rock High Yield-IVDMD‡ Cycle 1 (CIRC1)	Developed by USDA Grass Breeding project, Lincoln, NE using RRPS§.
Ey × FF High IVDMD Cycle 3 (HDMDC3)	Selected from Ey × FF base population for three cycles of high IVDMD by USDA Grass Breeding project, using RRPS.
Kanlow	Lowland type from central Oklahoma, developed by SCS PMC, Manhattan, KS.
Trailblazer	Selected from Ey × FF base population for one cycle of high IVDMD by USDA Grass Breeding project, using RRPS.

† Soil Conservation Service Plant Materials Center.
‡ IVDMD = *in vitro* dry matter digestibility.
§ Recurrent, restricted phenotypic selection.

applied on 17 April, 1991 and 0.6 kg a.i. ha^{-1} of bentazon (3-isopropyl-1*H*-2,1,3-benzothiodiazin-4(3*H*)-one 2,2-dioxide) was applied on 24 May, 1991. In 1992, alachlor, [2-chloro-2′,6′-diethyl-*N*-(methoxymethyl)acetanilide], at 2.2 kg a.i. ha^{-1}, and chlorsulfuron were applied at Mead on 1 May; 0.3 kg a.i. ha^{-1} of 2,4-D (2,4-dichlorophenoxyacetic acid) was applied at Mead on 6 May. Atrazine and metolachlor were applied on 4 March, at Ames; 2,4-D and metolachlor were applied at West Lafayette on 6 May.

Plots were sampled during vegetative growth stage and at heading. Forage was harvested at heading. Vegetative sampling dates were 13 June 1991 and 15 June 1992 at Mead, 20 June 1991 and 22 June 1992 at Ames, and 18 June 1991 and 17 June 1992 at West Lafayette. Vegetative samples were not collected from Kanlow plots at Mead and Ames in 1992 to allow sufficient growth for sampling at heading.

Samples were collected by cutting three to four tillers, at approximately 10 cm of height, from each plant within a plot. After drying in forced draft ovens at 50 °C (60 °C at West Lafayette), forage samples were ground in a Wiley[1] shear mill to pass a one mm screen and reground to uniformity in a cyclone impact mill. Samples were ground and analyzed at the USDA/ARS Forage Research Laboratory in Lincoln, NE. Growth stage of two to three tillers from each plant in a plot was determined using the system of Moore et al. (1991); estimated plot stage was the average stage of these tillers.

Heading date was determined as the day on which more than half of the plants in a plot had at least three panicles fully exserted above the flag leaf collar (R_3). For a given plot, a forage sample was collected on or shortly after heading date. The plot was then harvested at a height of approximately 10 cm with a flail plot harvester. Thus, harvest dates ranged from late June to late August each year. Disease ratings, with 0% being no disease visible and 100% being canopy death due to disease, and growth stage on a plot basis were recorded immediately before harvest. Stem rust, incited by *Puccinia graminis*, was the predominant disease. Dry weight of forage samples collected from vegetative growth and at heading was added to forage yield; the number of plants in each plot at harvest was determined and forage yield expressed as dry weight per plant. Regrowth was removed from plots with a flail plot harvester after killing frosts in autumn of 1991. At Ames in 1992, plots of the early maturing accession SD4 were sampled and harvested on 7 July while all other populations were sampled and harvested on 5 August. All other data were collected as in 1991.

Forage Quality Analysis

All samples were scanned with a near infrared reflectance spectrophotometer (Technicon Infralyzer 500, Bran & Luebbe Analyzing Technologies, Buffalo Grove, IL) over a wavelength range of 1100 to 2500 nm with 2-nm steps. Development and verification of prediction equations for IVDMD, NDF, ADF, and ADL based on wet lab values were as described by Hopkins et al. (1995). Laboratory values were used to develop NIRS prediction equations by using stepwise regression. Where possible, wet lab data used in developing and verifying NIRS prediction equations were obtained from samples originating from different blocks, locations, sampling stages, and populations. Prediction and verification sample sets contained, in approximately equal numbers, samples originating from the present research and from Hopkins et al. (1995). Sample sets used for prediction equation development and verification contained approximately 7 and 3%, respectively, of all samples from this experiment. Samples used for verification were not used in developing prediction equations. Hemicellulose was estimated as the difference between NDF and ADF, while cellulose was estimated as the difference between ADF and ADL.

[1] Names of products are included for the benefit of the reader and do not imply endorsement by the USDA or the University of Nebraska.

Statistical Analysis

Agronomic Data

Populations and blocks were assumed to be random effects, as were locations and years. Individual location-year combinations were analyzed as a randomized complete block. Data from individual locations were analyzed across years as a split plot in time with populations as whole plots, and years as split plots. Data from individual years were analyzed across locations as a nested factorial analysis (Hicks, 1973); blocks were nested within locations. Data were similarly analyzed across years and locations. Where needed, the method of Neter et al. (1985) was used to calculate approximate *F* values; approximate degrees of freedom were calculated according to Satterthwaite (1946). Expected mean squares and detailed ANOVA tables are reported by Hopkins (1993).

Forage Quality Maturity Adjustment

Maturity strongly influences switchgrass forage quality (Gabrielsen et al., 1990). Vegetative growth stage samples were collected on a given day and as a result the developmental stage at sampling often ranged from early jointing (E_1) to early head emergence (R_1). To minimize confounding of genotypic effects and G × E interactions with maturity, vegetative IVDMD data were adjusted to a uniform growth stage as follows. A *maturity* coefficient for vegetative digestibility was determined with raw data from both years and all locations by linearly regressing IVDMD against growth stage. Vegetative IVDMD alone was adjusted to a uniform growth stage, having been the only constituent with a significant ($P < 0.05$) maturity coefficient and a sizable coefficient of determination (R^2 = 0.32). The growth stage E_3 occurs just prior to the boot stage in switchgrass and was near the average growth stage at vegetative sampling. Individual plot data were adjusted to this growth stage with the following formula:

$$\text{Adjusted IVDMD} = \text{IVDMD} + [b \times (x - 2.65)] \quad [1]$$

where IVDMD is unadjusted vegetative digestibility, b is the maturity coefficient for vegetative IVDMD (in this case, 85.2), and x is observed plot stage. The growth stage E_3 is coded as 2.65 according to Moore et al. (1991).

Forage Quality Data

The same methods were used to analyze agronomic and forage quality data. Sampling stage for forage quality was assumed to be a fixed effect when included in the model. Individual location-year data were analyzed across samplings as a split plot in time with populations as whole plots and samplings as split plots. Forage quality data were subsequently analyzed by sampling stage because of consistent genotype by sampling interactions. Phenotypic correlations were calculated with raw data from all locations and years. All data were analyzed by Version 6 of the SAS software package (SAS Institute, 1990).

RESULTS AND DISCUSSION

Limited seed supply restricted the research to three locations. Differences in rainfall patterns and quantities,

Table 2. Seasonal climatic data, with deviations from 30 yr averages, for 1991 and 1992 at Mead, NE, Ames, IA, and West Lafayette, IN.

Location	Seasonal precipitation†		Monthly temperature†	
	Total	Deviation	Average	Deviation
	mm		°C	
		1991		
Mead‡	528	04	20.5	0.6
Ames	609	95	19.6	1.1
West Lafayette	323	−190	20.4	1.9
		1992		
Mead	379	−145	17.5	−2.4
Ames	456	−58	16.9	−1.5
West Lafayette	463	−50	16.9	−1.5

† Data are for 1 April–31 August.
‡ Nearest reporting stations with complete precipitation (Wahoo, NE) and temperature (Ashland, NE) data were used for Mead.

and in humidity levels, were expected to occur at the three locations. Weather conditions varied substantially during the research (Table 2).

Results were similar whether accessions were analyzed alone or with checks. Therefore, except where noted, the following results are based on analyses which included all 28 populations.

Agronomic Data

Across years and locations, significant ($P < 0.05$) variation among accessions for forage yield at heading was found along with a significant population × location × year (P × L × Y) interaction (Table 3). Likewise, variation among populations for forage yield at heading was significant at Mead and West Lafayette, with significant P × Y interactions at all locations (data not shown). Check strains generally produced greater amounts of forage than did accessions. Kanlow, Cave-in-Rock High Yield-DMD C1 (CIRC1), and Cave-in-Rock were among the highest yielding populations (Table 4). Accessions IA34 and IL62 were comparable in forage yield to check strains; MO3, MO18, and NE3 also tended to rank high among accessions for forage yield at heading. These accessions should be useful germplasm for breeding programs to develop improved switchgrass strains for livestock and/or biofuel production.

Rank correlations between locations for forage yield of accessions were significant in 1991 and 1992 (Fig. 2). These correlations can be attributed to accessions producing consistently large forage yields (IA34, IL62) while others produced consistently small forage yields (SD4 and IA48).

No variation among populations for disease rating was detected across locations and years; G × E interactions were also non-significant for this trait (Table 3). Disease incidence was rated highest at West Lafayette, averaging 32%. Greater disease ratings at West Lafayette may have been the result of greater disease pressure or differences in rating because the primary author recorded all disease ratings except those at West Lafayette which were recorded by K.D. Johnson. There was a significant ($P < 0.05$) but weak correlation ($r = -0.12$) between disease rating and forage yield at heading. For example, NE7 had the highest disease rating (25%) at Mead, but was also one of the higher yielding accessions at that location (Table 4). Early maturing strains, such as SD4, showed very little disease at heading, but had heavy stem rust infection on regrowth (data not shown).

Variation among populations for heading date was significant, as were all G × E effects for this trait (Table 3). Early maturity was often accompanied by low forage yield ($r = 0.65$). Averaged across years, Cave-in-Rock at West Lafayette was the only example of a population with a heading date before 20 July which produced more than 500 g plant^{-1} (Table 4).

Heading date for germplasm originating from more southern sites, such as MO16 and the check strain Kanlow, was consistently later (mid-August) than that of northern accessions such as SD4 and MN3 (late June). This result, along with similar observations reported for switchgrass collected from Nebraska (Eberhart and Newell, 1959) and from throughout the Great Plains (Cornelius and Johnston, 1941), demonstrate a strong photoperiod response of switchgrass. Such a photoperiod response may have affected the amount of genotypic variation observed in this research. For example, early

Table 3. Analysis of variance with mean squares for agronomic and forage quality traits of 23 switchgrass accessions and five check strains grown at three locations in 1991 and 1992.

Source	df	Heading date	Stem rust	Forage yield	Vegetative IVDMD†	IVDMD at heading
		d^2	$\%^2$	$(g/plant)^2$	$(g/kg)^2$	
Location	2	661.4	22 208.6*	1 954 253.3	1131.4	10 450.6
Block (L)	3	4.6	19.7	21 755.1	71.6	124.1
Population	27	1 629.1*	116.3	1 109 386.6*	361.8*	505.9
checks	4	1 777.6*	104.3	247 512.4	1103.7	614.4
accessions	22	1 398.9*	117.2	643 045.9*	322.1*	456.2
P × L	54	30.9*	87.8	83 812.9	83.2	399.3
P × B (L)	81	10.2*	51.1	23 740.0*	52.7*	99.0
Year	1	13 338.4	394.4	1 289 225.4	6556.7*	3 502.1
Y × L	2	30.9*	78.7	882 539.0*	220.4*	3 257.2
Y × B (L)	3	0.5	51.1	52 731.0*	20.1	528.9*
P × Y	27	39.1*	32.3	84 790.0	143.8*	215.8
P × L × Y	54	13.0*	56.9	103 689.5*	65.6*	261.8*
P × Y × B (L)	81	4.0	47.0	9 623.1	31.5	68.1

* Significant ($P < 0.05$).
† Data adjusted to a uniform growth stage.

Table 4. Means for yield and heading date (HD), averaged over 2 yr, for 28 switchgrass populations evaluated at Mead, NE, Ames, IA, and West Lafayette, IN.

Location and population	Yield	HD	Location and population	Yield	HD	Location and population	Yield	HD
	g plant^{-1}	d		g plant^{-1}	d		g plant^{-1}	d
	Mead			Ames			West Lafayette	
CIRC1	1531	206	CIRC1	919	203	Kanlow	1417	233
IA34	1377	214	Cave-in-Rock	883	205	IA34	1067	202
Trailblazer	1374	212	Kanlow	882	230	CIRC1	886	201
Kanlow	1364	234	IL62	833	208	Cave-in-Rock	804	198
Cave-in-Rock	1263	205	IA34	811	210	Trailblazer	793	201
HDMDC3	1160	215	Trailblazer	719	208	HDMDC3	776	203
IL62	1158	214	MO3	651	213	IL62	773	205
NE7	895	222	NE3	624	205	NE3	692	203
MO3	883	214	MO16	623	217	MO18	532	212
MO18	862	213	HDMDC3	612	215	NE7	528	207
MO19	831	214	IA26	603	206	MO19	464	209
IA57	810	203	MO18	576	216	IA57	451	206
NE3	763	207	IA57	559	202	MO16	446	213
MO16	745	221	MO19	555	213	MO3	430	212
IA31	694	200	SD2	464	194	IA31	385	195
IL1	436	202	IL60	442	193	SD2	365	192
IA41	395	203	IA31	441	199	IA26	326	199
IL60	389	201	MN3	428	191	MN3	242	190
SD2	376	195	IA25	387	190	MN4	221	188
MO6	375	204	IL1	374	195	IL60	202	193
IA26	363	204	IA37A	368	190	MO6	196	196
IA37A	347	191	IL3A	362	195	IL1	169	197
IA25	347	188	NE7	361	215	IA48	155	194
MN4	334	192	MO6	353	193	IL3A	154	194
MN3	332	189	IA41	318	199	IA25	131	193
IL3A	327	196	MN4	296	189	IA41	128	199
IA48	279	200	SD4	278	172	IA37A	121	191
SD4	107	172	IA48	269	194	SD4	75	170
SE	161	3	SE	184	3	SE	156	2
CV	45	2	CV	62	3	CV	67	2

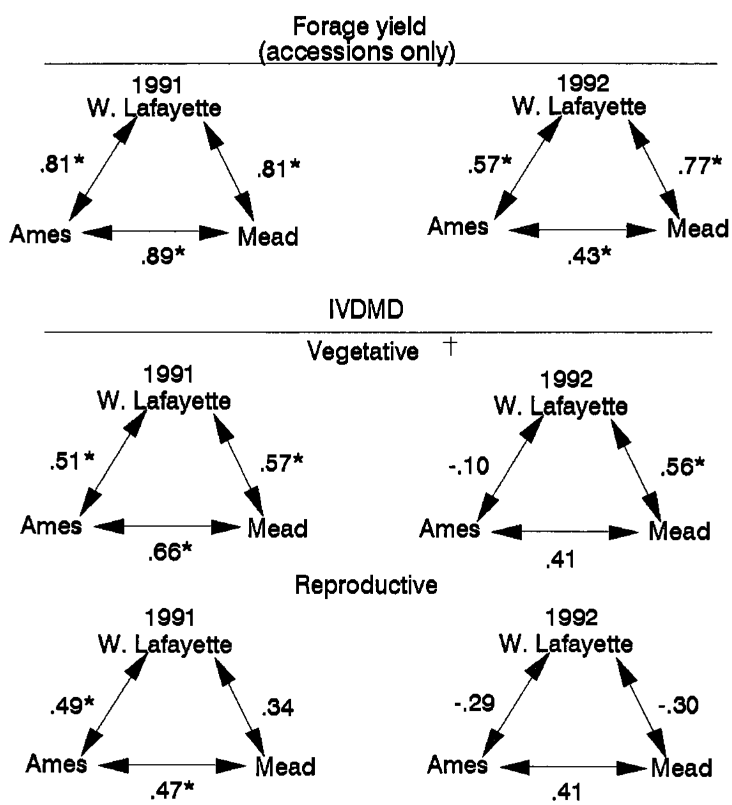

Fig. 2. Spearman rank correlations for yield and in vitro dry matter digestibility (IVDMD) of 23 switchgrass accessions. The symbols * and † indicate significance at $P < 0.05$ and adjustment to a uniform growth stage, respectively.

Table 5. Means, averaged over 2 yr, for digestibility (IVDMD) at a vegetative growth stage and at heading for 28 switchgrass populations grown at Mead, NE, Ames, IA, and West Lafayette, IN.

Location and population	Vegetative IVDMD†	IVDMD at heading
	g kg^{-1}	
Mead		
CIRC1	673	430
SD4	663	524
HDMDC3	662	466
MN3	662	499
IA34	647	407
NE3	645	419
IL3A	643	423
SD2	643	481
IA37A	642	512
MN4	637	516
Cave-in-Rock	637	403
MO19	636	412
MO16	631	434
IA25	630	462
IL62	629	398
IL60	629	438
IA57	626	414
IA41	625	444
Trailblazer	624	467
IA48	621	463
IA26	616	421
MO6	614	465
IA31	610	445
NE7	610	376
Kanlow	600	458
MO3	594	416
MO18	591	384
IL1	589	427
SE	16	26
CV	5	12

Location and population	Vegetative IVDMD†	IVDMD at heading
	g kg^{-1}	
Ames		
SD4	672	565
HDMDC3	665	557
Trailblazer	652	542
IA34	635	476
IL62	629	488
SD2	629	463
IA37A	627	453
NE3	626	521
MN4	621	450
MN3	620	474
CIRC1	619	490
MO19	619	493
NE7	617	491
IA31	608	538
IL3A	608	450
IA25	606	426
Cave-in-Rock	603	477
MO6	599	466
MO18	595	475
MO16	593	447
IA57	593	483
MO3	589	465
IL60	589	432
IA48	582	448
IA41	580	487
IA26	579	428
Kanlow	574	541
IL1	555	425
SE	20	32
CV	6	14

Location and population	Vegetative IVDMD†	IVDMD at heading
	g kg^{-1}	
West Lafayette		
CIRC1	657	507
SD4	652	554
IL60	646	516
MN3	637	530
IL3A	635	526
NE3	634	492
IA48	633	502
HDMDC3	631	521
MO19	628	512
IA26	625	507
SD2	625	522
Cave-in-Rock	624	492
IA57	624	497
IA37A	624	521
IA25	622	554
IA41	622	525
IL62	613	502
IA34	612	468
MO6	611	515
MO18	607	476
Trailblazer	606	502
MN4	605	530
Kanlow	602	458
NE7	599	492
IA31	599	458
IL1	597	486
MO3	592	476
MO16	591	445
SE	16	20
CV	4	8

† Adjusted to a uniform growth stage.

maturing populations might have achieved more of their yield potential farther north than the locations used in this experiment.

Forage Quality Data

Significant variation across locations and years was found among populations for IVDMD at the vegetative sampling (Table 3). There was also a significant P × L × Y interaction for vegetative IVDMD. For example, a significant rank correlation between Ames and West Lafayette occurred in 1991 but not in 1992 (Fig. 2). At each location, only SD4 consistently ranked among the top five populations for IVDMD at the vegetative growth stage (Table 5). Low ADL concentration was most closely associated with high IVDMD ($r = -0.71$) at this growth stage.

Across years and locations, variation among populations for IVDMD at heading was not statistically significant, perhaps because of a significant P × L × Y interaction (Table 3). For individual locations, variation among populations was significant only at Mead, with significant P × Y interactions at all locations (data not shown). In 1992, July was particularly wet, with West Lafayette receiving 282 mm, more than 10 times the rainfall amount for July, 1991. Temperatures were above normal in 1991 at all locations, while 1992 was cooler than normal (Table 2). At each location, average temperatures during June, 1991, were more than 2.5 °C warmer compared to those during June, 1992. Increased temperatures in controlled environment experiments have led to decreased digestibility in both warm season and cool season grass species (Wilson and Ford, 1971; Fales, 1986). Thus, variation in weather conditions occurring during this research may have contributed to G × E interactions. When data were analyzed by individual location and year, significant variation was found for IVDMD at heading in all instances except at West Lafayette in 1991 (data not shown).

The large G × E interactions for IVDMD at heading are illustrated by the relative performance of IA41 across years and locations. This accession ranked among the top two populations at Mead in 1991 (477 g kg^{-1}) but was among the bottom five populations at West Lafayette (484 g kg^{-1}) that same year. The situation reversed in 1992, with IA41 ranking among the bottom five group at Mead (411 g kg^{-1}), and among the top five populations at West Lafayette (566 g kg^{-1}). Rank correlations between locations for IVDMD at heading were low and mostly non-significant in 1991 and in 1992 (Fig. 2).

At each location, only SD4 consistently ranked among the top five populations for IVDMD at heading (Table 5). Averaged across years, this accession consistently had the earliest heading date (before 24 June) and produced the least forage (< 300 g plant^{-1}) at each location. In general, high IVDMD at heading was only slightly associated (r = -0.35) with low forage yield, and to a lesser extent ($r = -0.15$) with early heading date. Low ADL concentration was most closely associated with high IVDMD at heading ($r = -0.81$).

The primary cell wall constituents, hemicellulose plus cellulose (holocellulose) would be hydrolyzed to produce fermentable sugars in ethanol production from cellulosic biomass. Consequently, holocellulose yield is a potentially important biomass trait. For each population, holocellulose concentration at heading was greater than 670 g kg^{-1} of biomass, when averaged across years and locations. Such concentrations are similar to those for elite switchgrass populations grown in seeded stands at the same locations and years (Hopkins et al., 1995). Effective selection for increased forage yield at heading should result in increased holocellulose yield, provided there is not a substantial decrease in holocellulose concentration. Such a decrease seems unlikely, given that forage yield was not negatively associated with holocellulose concentration ($r = 0.14$).

Summary

This research demonstrates that genotypic variation for yield at heading, and IVDMD at a vegetative growth stage, exists among switchgrass accessions collected from remnant midwestern prairies. Across environments, variation among accessions for IVDMD at heading was often not significant, probably due to large G $\times$ E interactions associated in part perhaps with climatic differences.

Despite G $\times$ E interactions, a few accessions performed well across locations for forage yield at heading including IA34, IL62, and NE3. It should be possible, at a single location, to select for switchgrass accessions with forage yields comparable to those of cultivars and improved populations. This could then be followed by selection for IVDMD at heading within such better yielding accessions. It should be noted that single location selection for IVDMD at a reproductive growth stage was used by Vogel et al. (1981) to develop the widely adapted cultivar Trailblazer (Vogel et al., 1991).

Switchgrass accessions collected from remnant prairie sites in the midwest can provide useful genotypic variation for the development of populations with improved agronomic, forage quality, and biofuel traits.

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